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INTERACTION BETWEEN SENSORY AND POSTINGESTIONAL REPELLENTS IN STARLINGS: METHYL ANTHRANILATE AND SUCROSE[1]

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Abstract. Ingestion of concentrated sucrose solutions causes sickness in sucrase-deficient birds. As a result, some suggest that sucrose may represent an environmentally safe avian repellent. In the present experiments, we compared the repellency of sucrose to that of methyl anthranilate (MA), a known avian repellent. We also tested mixtures of sucrose and MA to investigate whether repellency could be enhanced, relative to sucrose or MA presented alone. The results showed that the MA was strongly avoided in both drinking and feeding trials. Conversely, only high sucrose concentrations were avoided, and only in drinking trials. No combination of MA and sucrose was as effective as MA alone. We conclude that sucrose is not sufficiently aversive to serve as an avian repellent in the field.

Key words: bird repellent; frugivory; fruit; learned aversion; methyl anthranilate; sensory irritant; starling.

INTRODUCTION

Birds cause significant losses to fruit growers (Mitterling 1965, Stevenson and Virgo 1971, Virgo 1971, Brown 1974, Tobin et al. 1989a). For example, nationwide estimates of blueberry losses are as high as 10% annually (Avery et al. 1992). In some instances, individual farmers can be more severely affected, depending on the location of an orchard and relative ripening time of the fruit. In particular, orchards near roosts are heavily damaged by birds (Brown 1974), as are early-ripening cultivars (Tobin et al. 1991).

Many of the available strategies for fruit protection are costly and frequently ineffective. For example, hazing will repel birds if properly implemented (Conover 1979, Summers 1985), but it is labor intensive and the costs are often not justified given the market returns for most fruit commodities (Dolbeer 1986). Use of netting to exclude birds also decreases crop losses, but it is difficult and expensive to protect large areas (Stuckey 1973, Foster 1979, Fuller-Perrine and Tobin 1992). Finally, although effective chemical repellents containing methiocarbamate have been available in the past (Guarino et al. 1974, DeHaven et al. 1979, Tobin et al. 1989b), the registration of methiocarb has expired and it will not be renewed (Tobin and Dolbeer 1987). With the loss of methiocarb there are no currently available nonlethal avian repellents registered by the Environmental Protection Agency for use in protecting fruit crops.

To meet growing needs for bird control, new strategies to protect fruits are being investigated. One such strategy is the development of bird-resistant varieties,

an approach that has been used with pears (Greig-Smith et al. 1983), maize (Dolbeer et al. 1988), and sorghum (Bullard et al. 1981). Recently, several investigators (e.g., Brugger and Nelms 1991, Brugger 1992, Brugger et al. 1992) have suggested that fruit varieties high in sucrose might be resistant to damage, because many passerines, including starlings (*Sturnus vulgaris*), waxwings (*Bombycilla cedrorum*), and robins (*Turdus migratorius*), lack the enzyme sucrase. Ingestion of concentrated sucrose solutions by sucrase-deficient birds causes sickness due to malabsorption (Martínez del Rio et al. 1988, 1989, Brugger and Nelms 1991). Because passerines can taste sucrose (Martínez del Rio et al. 1988, 1989, Brugger and Nelms 1991), Brugger and her colleagues have suggested that this sugar may represent an ideal repellent, providing both a sensory cue (conditional stimulus) and an environmentally safe aversive agent (unconditional stimulus).

Another promising strategy to reduce fruit depredation is the use of nonlethal sensory repellents such as methyl anthranilate (MA; Kare 1961, Mason et al. 1985, Glahn et al. 1989, Clark and Shah 1991, Clark et al. 1991, Cummings et al. 1991). Methyl anthranilate is an innately aversive irritant that stimulates trigeminal chemoreceptors (Mason and Silver 1983). Olfaction and gustation are not involved in the avoidance of this substance. Because MA rejection is mediated by pain, avoidance occurs as soon as the stimulus is perceived and prior to ingestion (Mason et al. 1989).

The distinction between a sensory repellent (one that is avoided because of intrinsic pain) and an associative repellent (one that is avoided because of learning) is heuristically important because avoidance elicited by them differs in several respects (Garcia et al. 1966, Mason and Reidinger 1983, Pelchat et al. 1983, Mason

1989, Mason et al. 1989, Sclafani 1991). For example, sensory repellents produce strong and immediate aversions that dissipate rapidly when the repellent is removed (Glahn et al. 1989). Conversely, animals learn to avoid associative repellents as a function of post-ingestive malaise, but once established, the avoidance response persists in the absence of the sickness-producing agent.

Because the mechanisms and behavioral parameters of sensory and associative repellents differ, combinations of the two might elicit a more immediate and durable avoidance than that elicited by either repellent type alone. The present experiments were designed to test this possibility. In addition, they also assessed whether synergy might cause mixtures of low MA and sucrose concentrations to yield an acceptable avoidance response. Reducing the amount of sucrose needed as an unconditional stimulus could prove especially beneficial because many fruits vulnerable to frugivory, e.g., grapes and cherries, have negligible amounts of this sugar (Widdowson and McCance 1935), and Brugger and Nelms (1991) and Brugger et al. (1992) have shown that only sucrose concentrations in excess of 11% reliably cause avoidance.

METHODS

Birds.—Adult European Starlings (*Sturnus vulgaris*) were captured using funnel traps during late spring at the Philadelphia Zoo. Birds were individually caged (61 × 36 × 41 cm) under a 12:12 light:dark cycle, with onset of light at 0700 Eastern Standard Time. Two weeks prior to testing, all birds were given free access to Purina Flight Bird Conditioner (Purina Mills, St. Louis, Missouri), water, and medicated oyster shell grit (United Volunteer Aviaries, Nashville, Tennessee).

Test system.—Starlings were used because previous experiments showed them to be sensitive to methyl anthranilate (MA; CAS number 25628-84-6; Clark et al. 1991, Mason et al. 1991). Furthermore starlings are a principal species damaging fruits in North American and Europe (Brown 1974).

Experiment 1: single-solution MA consumption.—We determined the starlings' concentration response curve for MA. Initially, tap water consumption by starlings was measured for 6 h, on each of three adaptation days. At the end of this period, individuals whose variance about the 3-d mean consumption was greater than ± 1 SD of the population variance were excluded from the trials. Those birds with stable daily water consumption were ranked according to mean water consumption and assigned to 1 of 8 groups. The bird with the highest water consumption was assigned to the first group, the bird with the second highest consumption was assigned to the second group, and so forth to the final group, followed by a series of assignments from the final group back to group 1. This procedure assured that all groups were balanced with respect to con-

sumption (Mason et al. 1991). A total of 48 birds were used for the experiment, with 6 birds per group. Groups were randomly assigned to receive different concentrations of MA on the day of treatment; these concentrations were: 1.0, 0.5, 0.1, 0.05, 0.01, 0.005, and 0.001% and a control at 0% (mass/volume).

After assignment to a concentration group, a 1-d pretreatment drinking trial was initiated. Beginning at 0930, tap water consumption was recorded once every 2 h (bihourly) for 6 h. The treatment period began at 0930 the next day, when birds were given their preassigned chemical treatment. Consumption was recorded every 2 h for 6 h. These timed observations allowed us to test for habituation effects. After the test, birds were given free access to tap water. During the posttreatment period on the following day, consumption of tap water was again recorded every 2 h for a total of 6 h. Posttreatment water consumption was compared with pretreatment water consumption to determine whether consumption returned to pretreatment levels.

Experiment 2: single-solution sucrose consumption.—Forty-two starlings were adapted to experimental conditions and assigned to seven groups ($n = 6$ birds/group) following the methods outlined in Experiment 1. Groups were randomly assigned to receive varying concentrations of a sucrose solution: 40, 20, 10, 5, 1, 0.1, and 0.01% (mass/volume), and given concentration response tests as described in Experiment 1.

Experiments 3–5: mixtures of MA and sucrose.—For each experiment (3–5) 36 starlings were adapted to experimental conditions and assigned to six groups ($n = 6$ birds/group) as described in Experiment 1. Birds were presented with mixtures of MA and sucrose. In Experiment 3, groups were presented with solutions containing 0.01% (volume/volume) MA mixed with sucrose solution at one of the following concentrations: 20, 10, 5, 1, 0.1 and 0.01% (mass/volume). Solutions were prepared in standard fashion. First, 10 mL of MA was placed in a volumetric flask, the appropriate mass of sucrose was added to the flask (i.e., 200 g for 20%), and then water was added to bring the volume to 1 L. The solution was magnetically stirred for 24 h, then sonicated. In Experiment 4 groups were presented with solutions containing 0.1% (volume/volume) MA mixed with sucrose at one of the following concentrations: 40, 20, 10, 1, 0.1, and 0.01% (mass/volume). In Experiment 5 groups were presented with solutions containing 1% (volume/volume) MA mixed with sucrose at one of the following concentrations: 40, 20, 10, 1, 0.1, 0.01% (mass/volume).

Experiment 6: habituation to sucrose consumption.—To test for the persistence of the conditioned aversion we presented birds with sucrose on each of 4 d and measured consumption during the 6-h test period. Thirty-six starlings were adapted to experimental conditions and assigned to six groups ($n = 6$ birds/

group) following the methods outlined in Experiment 1. Groups were randomly assigned to receive varying concentrations of a sucrose solution: 40, 20, 10, 1, 0.1, and 0.01% (mass/volume). During intertrial intervals tap water was available ad libitum.

Experiment 7: feeding trials. — We followed procedures detailed in Mason et al. (1989) for one-cup avian repellency evaluations. Because previous experience indicated that consumption was positively related to body mass we controlled for group differences in consumption by assigning 42 starlings to seven groups (n = 6 birds/group) on the basis of mass. The heaviest bird was assigned to group 1, the next heaviest to group 2 and so forth, with the eighth heaviest bird assigned to group 7, the ninth heaviest to group 6, and so forth. As a check we used a one-way analysis of variance to verify that there were no differences in consumption among groups. During the 3-d pretreatment period all food was removed from the cages within 1 h of light onset. Next a single cup containing 20 g of feed was placed in the front center of each cage, and consumption was recorded after 2 h. After testing and until light onset of the following day, birds had free access to feed. On the 4th d following the last pretreatment session, a 4-d treatment period began. Within 1 h of light onset, each group was given a cup with 20 g of feed treated with 0.1% MA + sucrose. The sucrose concentrations given to each group were randomly determined and were: 0.01, 0.1, 1.0, 5.0, 10.0, 20.0, and 40.0% (mass/mass). Preparation of food followed standard procedures. For example, for a 5% sucrose–food mixture, 5 g of sucrose was mixed with 5 mL of water and the solution was applied with an atomizer over the surface of the 95 g of food contained in a plastic tub. The atomizer was filled with 2.5 mL of water and the rinse was applied to the food. This process was repeated once more. The food was dried at 30°C for 24 h or to constant mass. The sucrose gave the bird chow a glazed appearance. The bird chow–sucrose mixture was weighed. Recovery was 99.91 ± 0.001% of the sum of the chow and sucrose mass. The missing mass was presumed to be loss of sucrose to the rat tub surface. The appropriate volume of MA was atomized onto the surface of the chow–sucrose glaze (volume/mass). As in the pretreatment period, consumption was measured after 2 h. At the end of the third treatment trial, birds were reweighed to assess whether any change from pretreatment mass had occurred. Birds were given free access to food and water during the next 4 d when a second treatment period was initiated. The seven groups were randomly assigned to receive food treated with sucrose alone at concentrations of: 0.01, 0.1, 1.0, 5.0, 10.0, 20.0, and 40.0% (mass/mass). Timing and conditions of the experiment were identical to those described above. After a 4-d intertreatment interval birds were again tested for a third treatment period. The seven groups were randomly assigned to receive food treated with MA alone, with group con-

centrations at: 0.001, 0.005, 0.01, 0.05, 0.1, 0.5, and 1.0% (mass/mass).

Analyses. — For Experiments 1–5 we tested the hypotheses that the total 6-h water consumption did not differ among treatment days or treatment concentration groups. The data were analyzed using a repeated-measures analysis. Variability due to difference between subjects can be eliminated from the experimental error using a repeated-measures design. The specific designs used are ideally suited to look for carry-over effects (i.e., the effect of the previous day on the current day's performance). We used a two-factor ANOVA with repeated measures on days, with three levels (day 1 = pretreatment, day 2 = treatment, and day 3 = posttreatment). The between-subjects factor was treatment concentration group. Post hoc differences among means ($P < .05$) were determined using a Tukey's B test. For Experiment 6, we tested the hypotheses that water consumption did not differ across periods (pretreatment and treatment), days (1–4 within each period), or treatment concentration groups. Because each of four test days were nested within two different types of treatment periods we analyzed the data using a split-plot approach to a repeated-measures analysis. To use the univariate approach we tested the assumption that the covariance matrix of the transformed variables had a constant variance on the diagonal and zeros off the diagonal. We found that Mauchly's test of sphericity was not significant, thus further analyses did not require adjustments of the degrees of freedom and were based upon averaged univariate F tests. The between-subjects factor was treatment concentration groups. Interactions consisted of concentrations × days within period effects, and days within period effects. For Experiment 7, we tested the hypotheses that consumption of treated food did not differ across days (four levels), concentration groups (seven levels), or treatments (three levels: MA alone, MA with sucrose, and sucrose alone). Data were analyzed using a three-factor ANOVA with repeated measures on days. Unless otherwise indicated, all data were tested and found to be homogeneous using the Bartlett–Box method.

RESULTS

Drinking trials: total 6-h water intake

Experiment 1. Single solution: MA. — The consumption pattern for the groups differed across days ($F = 8.61$, df = 14, 116, $P < .001$). Intake of treated water decreased as a function of increasing concentration of MA. There were no carry-over effects, as evidenced by the similarity of the consumption profiles for the pre- and posttreatment periods (Fig. 1A). These data are similar to consumption patterns observed in previous tests (Clark et al. 1991). Considering treatment day alone, post hoc analysis showed that the two highest concentration groups, 1 and 0.5% drank similar
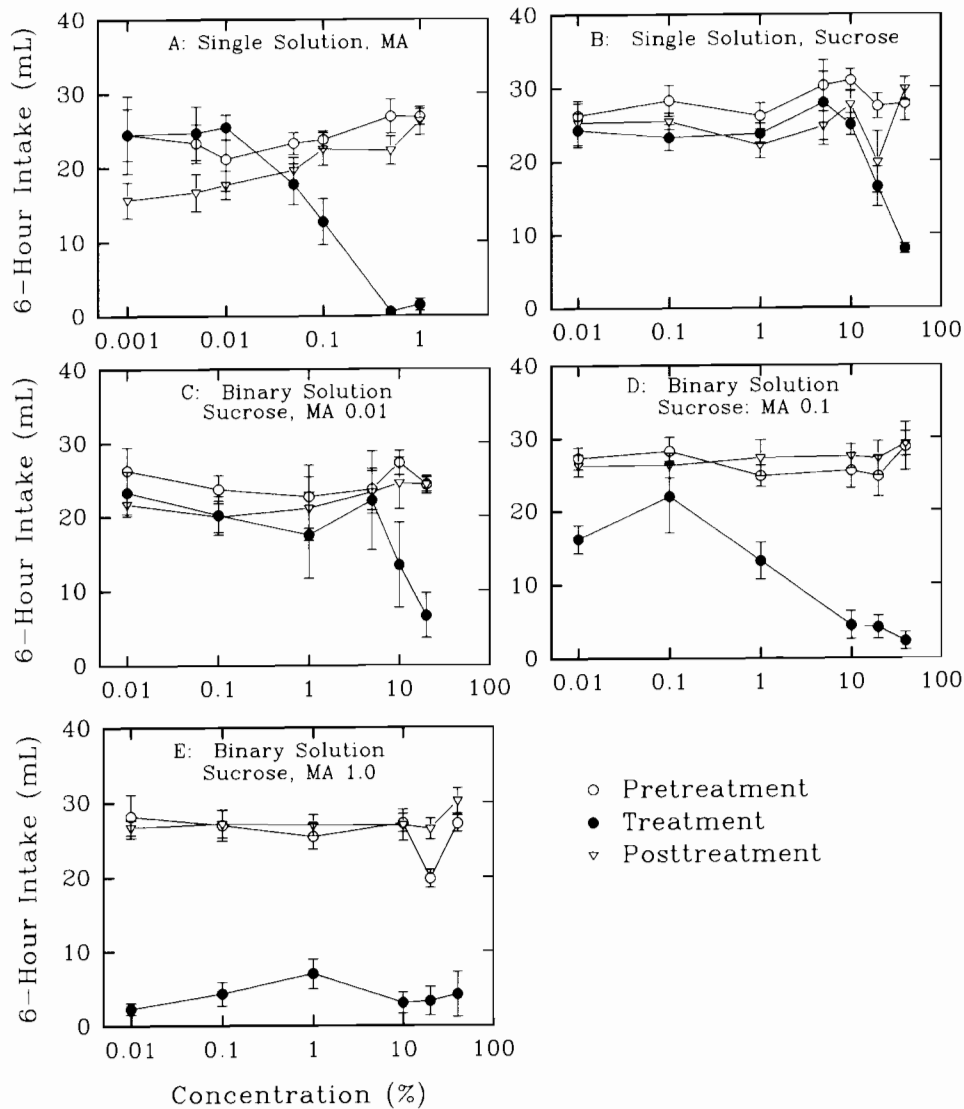
FIG. 1. Total fluid consumption for 6-h trials. (A) Experiment 1, where birds were presented with solutions containing methyl anthranilate (MA) alone. (B) Experiment 2, where birds were presented with sucrose alone. (C) Experiment 3, where birds were presented with a binary solution of 0.01% MA in combination with a predetermined concentration of sucrose. (D) Experiment 4, where birds were presented with a binary solution of 0.1% MA in combination with a predetermined concentration of sucrose. (E) Experiment 5, where birds were presented with a binary solution of 1% MA in combination with a predetermined concentration of sucrose. Data are means ± 1 SE.

amounts, but significantly less than all other concentration groups. The remaining concentration groups, including the 0% control group (mean ± SE = 23.7 ± 2.6 mL, Fig. 1A), exhibited similar intake, though there was a tendency for the 0.05 and 0.1% groups to consume relatively less solution. Water intake among the concentration groups was equal within each of the pretreatment and posttreatment periods.

Experiment 2. Single solution: sucrose. — The consumption pattern for concentration groups also differed across days in the single-solution sucrose test ($F = 5.1$, df = 12, 70, $P < .001$). Birds exposed to higher concentrations of sucrose drank less solution (Fig. 1B). No

long-term effects on fluid intake were evident, i.e., water consumption during the posttreatment period returned to pretreatment levels. The post hoc test showed that only the intake for the 40% sucrose solution was different from that of the other treatment groups.

Experiment 3. Binary solution: 0.01% MA with varying sucrose concentration. — Consumption by concentration groups also differed across days, with intake of binary solutions on the treatment day decreasing as a function of increasing sucrose concentration (Fig. 1C; $F = 2.28$, df = 10, 60, $P = .024$). The post hoc test for the treatment day showed that the group receiving the 40% sucrose concentration differed from all other treat-

ment groups except from the group receiving 20% sucrose. There were no other differences among groups for the treatment day. Furthermore, there was no carryover effect as a consequence of drinking any of the binary solutions. Consumption across all groups during the posttreatment period returned to pretreatment levels.

Experiment 4. Binary solution: 0.1% MA with varying sucrose concentration.—Intake differed across days as a function of sucrose concentration, with consumption of the binary solution decreasing as a function of increasing sucrose concentration ($F = 5.28$, df $= 2$, 60, $P < .001$). In contrast, intake of water during the pre- and posttreatment periods was normal and similar across groups (Fig. 1D). This indicated the absence of carry-over effects resulting from binary fluid intake. The post hoc test for the treatment day indicated that intake for the three highest sucrose solutions was similar and differed from intake levels for groups receiving lower concentrations of sucrose. There were no other differences among groups.

Experiment 5. Binary solution: 1% MA with sucrose.—The pattern of consumption across treatment concentration groups and for each of the test days was constant ($P = .178$). However, intake during the treatment day was considerably lower than during either the pre- or posttreatment periods (Fig. 1E; $F = 355$, df $= 2$, 60, $P < .001$). The post hoc test within the treatment period indicated that all treatment concentration groups had equal consumption. No level of sucrose blocked the expected suppression of consumption of a 1% solution of MA (compare Fig. 1B and A at 1% MA).

Summary of Experiments 1–5: comparison of solutions.—Overall, increasing concentrations of MA in binary solutions caused a leftwards shift in the fitted intake curve relative to the solution containing sucrose alone. In addition, increasing the MA content of a binary mixture minimized intake for a wider range of sucrose concentrations (Fig. 2), as indicated by an elongation for the lower asymptotic consumption. Increasing concentrations of MA also resulted in a depression of the upper and lower asymptotic consumption levels relative to the sucrose response curve, i.e., a downward shift in the concentration response curve.

Summary of Experiments 1–5: 2-h consumption patterns.—Sensory avoidance of fluid is characterized by a constant low intake over time. This absence of habituation was observed each time starlings were exposed to high concentrations of MA (0.5–1.0%), either in a single solution (Fig. 3A) or in a binary solution (Fig. 3E). In the latter case, bihourly intake was only slightly higher than would be expected from a solution containing MA alone. For low concentrations of MA in single-solute fluids, birds consumed liquid in inverse proportion to MA concentration, but they did not show signs of habituation (Fig. 3A).

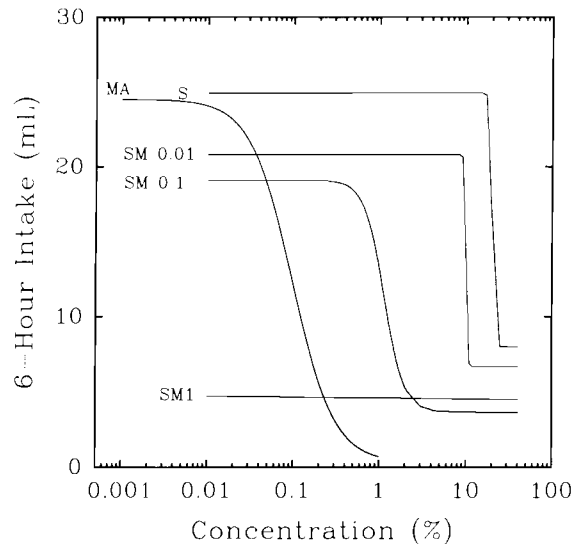Alternatively, postingestional learned adversions are

FIG. 2. Fitted curves for 6-h fluid intake as a function of concentration (all concentrations as mass/volume). MA = methyl anthranilate, S = sucrose, SM 0.1 = binary mixture of various concentrations of sucrose with 0.01% MA, SM 0.1 = binary mixture of various concentrations of sucrose with 0.1% MA, SM 1 = binary mixture of various concentrations of sucrose with 1% MA. Curves were fitted using a nonlinear four-parameter logistic equation.

characterized by high initial intake and lower subsequent consumption. This was evident for the single-solute sucrose solutions, where sucrose concentration was ≥20% (Fig. 3B). However, starlings exposed to lower sucrose concentrations (≤10%) showed no signs of a conditioned aversion (Fig 3B). In fact, consumption for birds exposed to single-solute solutions of ≤10% was within the range of bihourly fluid intake for controls.

There was evidence of synergism for binary solutions. Starlings exposed to at least 20% sucrose in combination with 0.01% MA showed a substantial suppression of fluid intake within the first 2 h (Fig. 3C) when compared to single-solute solutions of equal concentration (Fig. 3A, B). Prolonged exposure increased the aversive response, indicating that bird learned to avoid the solution as well. Lower concentrations of sucrose (≤10%) failed to interact with 0.01% MA in a similar strong fashion. Increasing the concentration of MA to 0.1% in a binary solution enhanced the repellency of sucrose and MA, but the pattern of bihourly fluid intake indicated that sensory effects were largely responsible for reduced consumption (Fig. 3D).

Experiment 6. Fluid intake after repeated exposure to sucrose solution.—Intake among concentration groups was similar across days during the pretreatment period ($P = .519$), but differed across days among the sucrose concentration groups during the treatment period ($F = 1.91$, df $= 15$, 90, $P = .032$). Birds exposed to high levels of sucrose (≥20%) consumed less solution than birds exposed to lower levels of sucrose
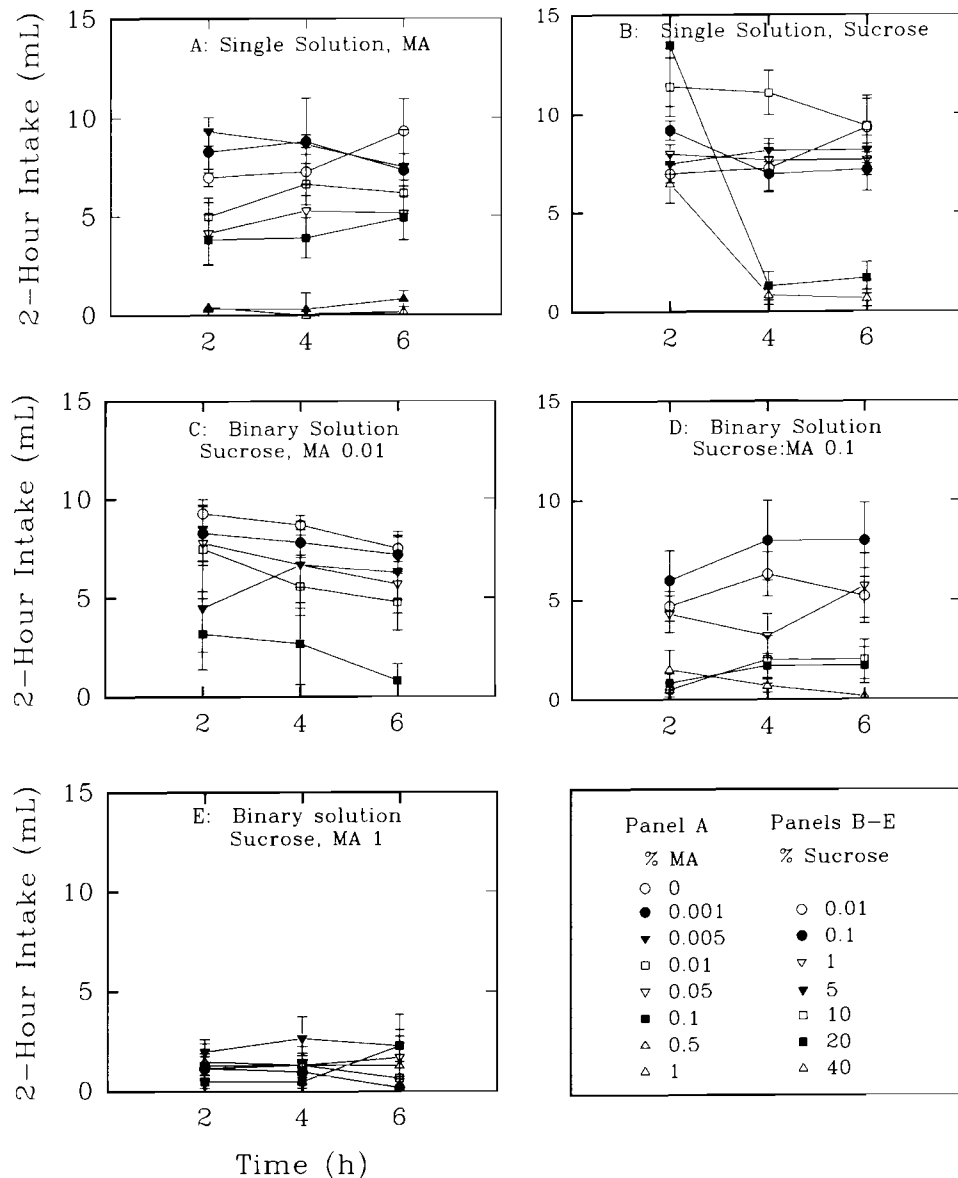
FIG. 3. Bihourly fluid intake. (A) Experiment 1, where birds were presented with solutions containing MA alone. (B) Experiment 2, where birds were presented with sucrose alone. (C) Experiment 3, where birds were presented with a binary solution of 0.01% MA in combination with a predetermined concentration of sucrose. (D) Experiment 4, where birds were presented with a binary solution of 0.1% MA in combination with a predetermined concentration of sucrose. (E) Experiment 5, where birds were presented with a binary solution of 1% MA in combination with a predetermined concentration of sucrose. Data are means ± 1 SE.

($\leq$10%; Fig. 4). Of interest is the tendency for birds in the groups exposed to 20% and 40% sucrose to increase their fluid intake by the 4th d. The increased fluid intake represented a slight but incremental increase in consumption by all members of the group.

Experiment 7. Feeding trials.—There were no differences among groups in feed consumption during the pretreatment period ($F = 0.47$, df = 6, 28, $P = .824$). Overall, mean feed consumption for all groups was 4.6 ± 0.094 g. During the test period, there was a signif-

icant concentration effect for food treated with MA (Fig. 5; $F = 7.54$, df = 6, 28, $P < .001$). Post hoc tests showed that intake of the highest MA concentrations (1 and 0.5%) was less than that of concentrations ranging from 0.001 to 0.05%. There were no differences for food consumption among concentration groups in the sucrose trials ($F = 2.15$, df = 6, 28, $P = .079$). Intake for all birds averaged 5.6 ± 0.14 g. Adding 0.1% MA to different sucrose concentrations did not alter intake. Birds showed the same pattern of consumption across

days for all binary mixtures of MA and sucrose con-
centrations ($P = .61$). Overall, there was no concen-
tration effect of the binary mixture ($P = 4.72$), though
there was a tendency for birds to consume more feed
as the trial progressed ($F = 27.65$, df $= 2$, 56, $P <$
.001).

DISCUSSION

Because irritants are painful, animals rarely become
accustomed to them in foods and fluids: avoidance
tends to remain constant as long as the irritant is de-
tected. This constancy (or lack of habituation) was ob-
served in the present experiments whenever starlings
were exposed to high concentrations of MA (0.5–1.0%).
Although avoidance was detected for both simple so-
lutions and mixtures, intake of mixtures containing any
given MA concentration was slightly higher than con-
sumption of MA presented alone.

Unlike avoidance mediated by irritation, avoidance
mediated by postingestional malaise is characterized
by high initial intake and lower subsequent consump-
tion. This pattern was observed when sucrose alone
was presented at concentrations $\geq 20\%$. Sucrose was
not a strong unconditional stimulus, however, as star-
lings exposed to relatively low sucrose concentrations
($\leq 10\%$) drank the same amount during treatment as
birds presented with plain tap water.

When the highest sucrose concentrations were mixed
with the lowest MA concentrations, some evidence of
synergy was obtained. When compared with single-
solute solutions of equal concentration, starlings ex-
posed to $\geq 20\%$ sucrose in combination with 0.01%
MA showed a substantial suppression of fluid intake
within the first 2 h. Prolonged exposure increased the
aversive response, indicating that birds learned to avoid
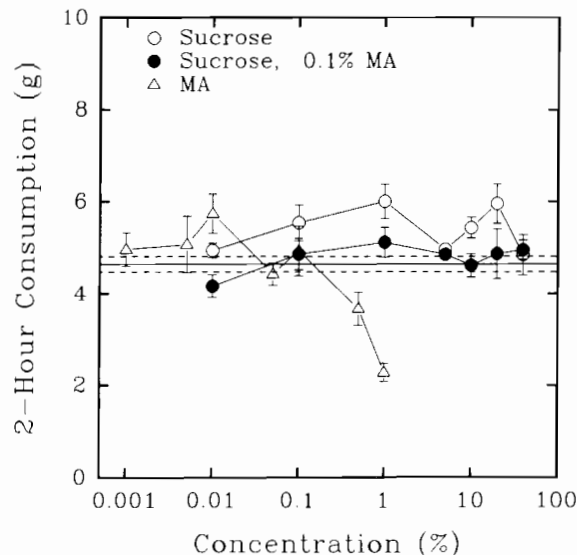the solution as well. Lower concentrations of sucrose

FIG. 5. Food intake (averaged over 3 d) during a 2-h test
period. Data are means $\pm$ 1 SE.

($\leq 10\%$) failed to interact with 0.01% MA in a similar
strong fashion. Increasing the concentration of MA to
0.1% in the binary solutions enhanced repellency, but
the pattern of bihourly fluid intake indicated that MA
only was largely responsible for reduced consumption
(i.e., responses to the mixture were not substantially
different than to MA alone).

Overall, the present results suggest three principal
conclusions. First, as demonstrated in many other lab-
oratory and field studies (Kare 1961, Mason et al. 1985,
Glahn et al. 1989, Clark and Shah 1991, Clark et al.
1991, Cummings et al. 1991), MA is a reliable sensory
repellent. Second, relative to other substances that cause
learned food avoidance (Garcia et al. 1966, Mason and
Reidinger 1983, Pelchat et al. 1983, Mason 1989, Scla-
fani 1991), sucrose is a weak unconditional stimulus
(i.e., it is only effective at high concentrations). Third,
although some evidence of synergy was obtained, the
overall effect of mixing MA with sucrose was a dimi-
nution in the effectiveness of the MA. This observation
is consistent with mammalian psychophysical data that
suggest that avoidance is significantly weakened when
an irritant is presented in a solution containing a taste,
and especially when that taste is sucrose (Stevens and
Lawless 1986).

MANAGEMENT IMPLICATIONS

*Sucrose as an associative repellent for sucrase-defi-
cient birds.*—Brugger and Nelms (1991) suggest that
enhanced sucrose concentrations in fruit and/or topical
applications of sucrose, per se, could deter depredation
by sucrase-deficient birds. Although these propositions
cannot be discounted, the results of Experiment 2 call
both into question. In the present experiment, learned
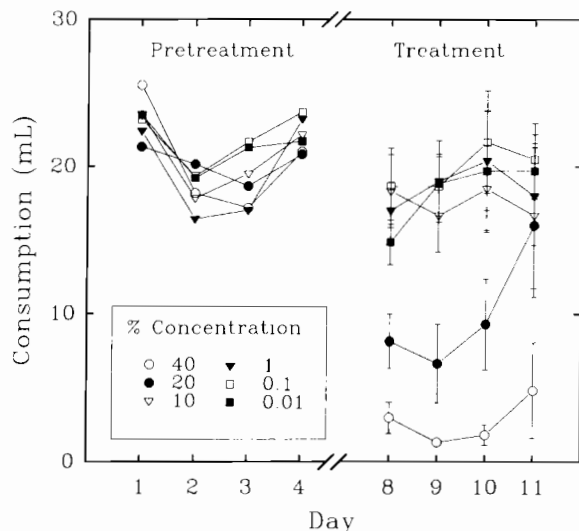aversions to sucrose were observed only when concen-

FIG. 4. Fluid intake of sucrose solutions over time. Treat-
ment values are means $\pm$ 1 SE.

trations exceeded 20%. This rejection threshold is comparable to that reported by other investigators (Schuler 1983, Martínez del Rio et al. 1988), and almost 250% higher than the highest concentrations known to occur in fruits (8.5%; Widdowson and McCance 1935). Although fruits containing sucrose could conceivably be bred to double or triple their sucrose content and fruits that do not contain sucrose (e.g., grapes, cherries) could be engineered to produce that sugar, the practical application of endogenous sucrose as an avian repellent seems remote.

If sucrose were topically applied, e.g., as an antidesiccant, to fruits otherwise low in sucrose, the number of treated fruits necessary to cause food avoidance learning would be unrealistically large. In the present experiments, conditioned aversions to solutions were reliably acquired only when starlings received sucrose loadings ≥ 1.6 g/h. Assuming 0.1 mL of a 20% solution is sufficient to coat a cherry, a starling would have to consume 80 cherries (i.e., 320 g of fruit) in an hour to ingest sufficient sucrose to cause learning.

Sucrose and MA mixtures as avian repellents. — Although no sucrose concentration or sucrose–MA mixture was as aversive as MA alone, mixtures containing large amounts of sucrose and small amounts of MA (i.e., 0.01–0.1%) were more aversive than high sucrose solutions, per se. This result suggests that fruit need not contain extremely high sucrose concentrations ($\geq 3\%$ sucrose might suffice) in order to repel birds, provided that weak MA solutions are topically applied. Whether such combinations are practical, however, can be questioned on several grounds. No sucrose concentration was high enough to elicit avoidance of feed, and in drinking trials, birds who showed initial avoidance of high sucrose concentrations tended to increase fluid intake by the 3rd and 4th d of exposure. This latter finding is opposite to the results of Brugger et al. (1992). Joined with the former result, these data highlight the potential importance of the context in which sucrose is ingested. In the present experiments, feed was freely available during all drinking trials. Such was not the case in investigations reported by Brugger et al. (1992). We suggest that the absorption of salts or other nutrients from the feed, and the consequent transport of water, counteracted the osmotic effects of unabsorbed sucrose. As a result, the starlings may have learned to consume feed to abate malaise. This possibility is consistent with findings for mammalian species, although it has not been reported previously for birds (Zahorik 1976). If starlings can acquire such behaviors in the laboratory, then we speculate that they would be able to acquire it in the field.

It is important to note that the present experiments do not address factors such as the long-term effects of sucrose in the avian diet and how such loads might affect foraging profitability by influencing assimilation efficiencies (Martínez del Rio 1990). Nor do the data address how addition of conditional stimuli such as

color cues (Mason 1989) or odors might affect short-term repellency. Nevertheless, while cautious about speculating from the laboratory to the field, we suggest that endogenous sucrose and/or topical applications of sucrose appear to have limited value as potential bird repellent strategies.

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